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Pollinator genetics and pollination: do honey bee colonies selected for pollen-hoarding field better pollinators of cranberry *Vaccinium macrocarpon*?

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Abstract. 1. Genetic polymorphisms of flowering plants can influence pollinator foraging but it is not known whether heritable foraging polymorphisms of pollinators influence their pollination efficacies. Honey bees *Apis mellifera* L. visit cranberry flowers for nectar but rarely for pollen when alternative preferred flowers grow nearby.

2. Cranberry flowers visited once by pollen-foraging honey bees received four-fold more stigmatic pollen than flowers visited by mere nectar-foragers (excluding nectar thieves). Manual greenhouse pollinations with fixed numbers of pollen tetrads (0, 2, 4, 8, 16, 32) achieved maximal fruit set with just eight pollen tetrads. Pollen-foraging honey bees yielded a calculated 63% more berries than equal numbers of non-thieving nectar-foragers, even though both classes of forager made stigmatic contact.

3. Colonies headed by queens of a pollen-hoarding genotype fielded significantly more pollen-foraging trips than standard commercial genotypes, as did hives fitted with permanently engaged pollen traps or colonies containing more larvae. Pollen-hoarding colonies together brought back twice as many cranberry pollen loads as control colonies, which was marginally significant despite marked daily variation in the proportion of collected pollen that was cranberry.

4. Caloric supplementation of matched, paired colonies failed to enhance pollen foraging despite the meagre nectar yields of individual cranberry flowers.

5. Heritable behavioural polymorphisms of the honey bee, such as pollen-hoarding, can enhance fruit and seed set by a floral host (e.g. cranberry), but only if more preferred pollen hosts are absent or rare. Otherwise, honey bees' broad polylecty, flight range, and daily idiosyncrasies in floral fidelity will obscure specific pollen-foraging differences at a given floral host, even among paired colonies in a seemingly uniform agricultural setting.

Key words. *Apis*, Apoidea, bees, behavioural genetics, cranberry, foraging, pollination efficiency, pollinator, *Vaccinium.*

Introduction

An individual pollinator's contribution to sexual reproduction by its floral host(s) is defined largely by its foraging behaviours. These include taxonomic fidelity, resource selection, grooming frequency, tendency to rob or thieve nectar, interfloral flight distance, posture and positioning while on a flower, daily foraging schedule, and more (reviewed in Linsley, 1958; Wcislo & Cane, 1996). Many of these attributes have a predictable species-specific component; for instance, some species of bumble bees regularly rob flowers (i.e. remove nectar without stigmatic contact) while others rarely rob flowers (Ranta, 1983). Heritable differences or polymorphisms in such behavioural

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phenotypes should be of potentially great consequence for pollination. A few heritable polymorphisms of pollinators are known to influence their own reproductive fitnesses, such as wing pigmentation of butterflies (e.g. Stimson & Berman, 1990; Nielsen & Watt, 1998) and the hygienic behaviours of honey bees (reviewed in Moritz, 1988); however, no report of a behavioural polymorphism of a pollinator has been shown to influence reproduction by its mutualistic partners, the flowering plants, although there are several tantalising but incomplete examples of foraging genotypes for the honey bee *Apis mellifera* L. (e.g. Mackensen & Nye, 1969; Guzman-Novoa & Gary, 1993).

Among invertebrate pollinators, genetic polymorphisms that influence floral foraging behaviours have been documented only for the honey bee. Foragers from different patrilines living in the same colony exhibit heritable variation in their preferred foraging distances (Oldroyd *et al*., 1993), numbers and durations of pollen-foraging trips, nectar volume loads (Guzman-Novoa & Gary, 1993), and perhaps even floral hosts (Oldroyd *et al*., 1992), as well as in their propensities to gather nectar or to hoard pollen (reviewed by Page *et al*., 1995). Honey bees, which typically eschew alfalfa pollen (= lucerne *Medicago sativa* L.), were bred successfully to prefer foraging at this pollen source in just six generations of selective breeding (Mackensen & Nye, 1969) but the stock's value for pollination was never determined.

Colonies depend on pollen for all their dietary protein and lipid needs; pollen is eaten directly or packed in cells of the wax comb for later retrieval. A colony's foraging force will gather more pollen in response to experimental interception of incoming pollen (Webster *et al*., 1985), depletion of its pollen stores (Fewell & Winston, 1992), or addition of hungry uncapped larvae (*brood*) (Free, 1967).

In addition to environmental cues that stimulate pollen foraging and hoarding, there is also a considerable genetic component in the variation of pollen collection and storage behaviours (e.g. Mackensen & Nye, 1969). Artificial selection for differing degrees of pollen hoarding by colonies can achieve marked divergence of this trait in only four to five generations (Hellmich *et al*., 1985). Two major quantitative loci have been shown to exert a strong influence on both a colony's degree of pollen hoarding and the likelihood that an individual forager will return with pollen (Hunt *et al*., 1995).

In contrast with flowering plants, far less is known about heritable polymorphisms of pollinators that can influence the outcomes of their reproductive interactions with flowering plants, such as the probabilities of fruit and seed set. Without such evidence for heritable variation in pollinator foraging behaviours as well as floral attributes of their plant hosts, co-evolution remains an unlikely means for moulding traits of interacting plants and their pollinators. In the work reported here, colonies of honey bees bred to express a supernormal pollen-hoarding genotype (hereafter called *pollen-hoarding*) were evaluated against a standard genotype for their forager's individual and collective contributions to fruit set by the American cranberry *Vaccinium macrocarpon* Aiton (Ericaceae).

Materials and methods

Stigmatic pollen threshold for fruit set

Reproductive, upright stems of the cranberry cv 'Stevens' were cut from a producing cranberry bed near Chatsworth, New Jersey, U.S.A. (39°49′N, 74°31′W) during July 1995 and rooted individually in forestry propagation cells (Cone-tainers from Stuewe & Sons, Inc., Corvallis, Oregon). The rooting and growing medium was a standard mix of sand and peat used in cranberry propagation. Plants were allowed to go dormant in an unheated greenhouse during autumn 1995, and moved to a heated greenhouse the following April. Day length was extended to 14 h by means of artificial lighting. The same plants were used for experimental manual pollinations in 1996 and 1997.

For each rooted cutting, one flower bud was emasculated (to prevent auto-pollination) and remaining flowers and buds were removed. Flowers were deemed receptive when fluid was visible on the stigma, typically 4 or 5 days after emasculation. On each pollination date, fresh pollen was gathered on a glass slide from open flowers of compatible cv 'Early Black' (1996) or 'Stevens' (1997). Cranberries are largely self-compatible but optimal fruit and seed set is achieved when the vegetatively propagated cultivars are crossed (Sarracino & Vorsa, 1991). Individual plants in their propagation cells were inverted under a stereomicroscope so that the surface of each emasculated flower's stigma was upright and visible. Precise counts of pollen tetrads (0, 2, 4, 8, 16, and 32) were transferred to a receptive stigma using a single-hair brush. Stigmatic pollen loads were assigned randomly to individual flowers within a replication of the experiment. Following pollination, plants were held in the greenhouse and scored for fruit set after 90 days. Fruit size and seed set will be reported in detail elsewhere (D. Schiffhauer and J. H. Cane, unpublished). The probability of fruit set was fitted to pollen tetrads per stigma by nonlinear regression (SigmaPlot 4.0, SPPS Inc., Chicago, Illinois). *G*-tests of independence were applied to the overall experiment and to selected combinations of pollen tetrads per stigma and resultant fruit set (Sokal & Rohlf, 1995).

Pollination by individual honey bees

To evaluate the consequences of a honey bee's foraging behaviour for cranberry pollination, a five-frame nucleus colony was moved to a 48-m^3 field cage set over a bog near Chatsworth, New Jersey with blooming 'Early Black' cranberries. Confinement deprived the colony of alternative pollen sources, thereby favouring pollen-harvesting from cranberry. An 8-m^2 patch of blooming cranberry was kept free of bee visitation using polyester floating row cover. Six days after initial confinement, on 26 June, the row cover was pulled back at 14.00 hours to allow foraging honey bees access to these reserved, virgin flowers.

Virgin flowers receiving single legitimate visits from honey bees were gently clipped, inverted, and placed in a well of an ELISA plate to return to the laboratory. Flowers were classed

as either drummed by pollen-foragers (Cane *et al*., 1993) or visited for nectar only. Honey bees and leaf-cutting bees (Megachilidae) that use their legs to batter a cranberry flower's staminal column are effective in releasing pollen that is otherwise withheld by the anther's terminal pores (Cane *et al*., 1996). Flowers visited without stigmatic contact were discarded. In the laboratory, stigmas were squashed individually on microscope slides in acetocarmine jelly, and the total numbers of pollen tetrads were counted. The average numbers of pollen tetrads deposited on stigmas by pollen- or nectar-foraging honey bees were compared using a two-tailed *t*-test for unequal variance (SAS, 1989). Pollen- and nectar-foragers were also compared for the proportion of their visits that delivered at least eight pollen tetrads, using a *G*-test with Williamson's correction (Sokal & Rohlf, 1995). Eight tetrads (= 32 pollen grains) is the minimum number needed to achieve maximum fruit set in the greenhouse pollination trials (see Results).

Pollen foraging by honey bee colonies

Eighteen colonies, half headed by queens of the pollen-hoarding genotype, the remainder a mix of three commercial lines used by a collaborating migratory beekeeper, were established at the margins of three adjoining commercial cranberry bogs near Chatsworth, New Jersey. Queens of the pollen-hoarding strain were obtained from the selected stock maintained at the University of California at Davis (Page & Fondrk, 1995). Control queens came from several commercial sources. All 18 queens had been newly installed 3 months earlier. Each hive consisted of a single deep and shallow super. Each hive was sealed with tape and set on top of a bottom board pollen trap made to Ontario Agricultural College-style dimensions (Stauffer's Beehives Inc., Port Trevorton, Pennsylvania). Pollen traps were engaged five times for all colonies during 24–48-h periods of favourable foraging weather over the next 11 days. Trapped pollen was swept out of each trap and into tightly sealed individual plastic bags set in a cooler and later weighed. Scopal pollen pellets recognisable as cranberry (checked microscopically) were separated from all other pellets (e.g. *Nuphar*, *Rubus*, *Nymphaea*) and weighed, allowing calculation of the fraction of intercepted pollen that was cranberry.

Colony strength was evaluated 8 days after the end of the experiment to avoid disrupting colony activities during the experiment. All frames were removed from each colony, and the area of capped brood estimated for each side of every comb as a rectangle whose edges were measured to the nearest centimetre using a clear ruler. This capped brood would have been actively growing larvae being fed with pollen and honey during the preceding days of experimentation. The total area of brood is a good estimate of relative colony strength and larval food demand during an experiment (Webster *et al*., 1985).

Colonies headed by queens of pollen-hoarding and commercial genotypes were compared for both total pollen influx and the influx of just cranberry pollen. Total pollen influx was compared by ANCOVA, where the covariate was the area of capped brood measured per colony. Cranberry pollen influx was compared using a repeated measures ANCOVA, for which each day's weight of trapped cranberry pollen per colony was used, and the covariates were brood area and fidelity (Proc GLM, SAS, 1989). Weights of trapped pollen were log-transformed to minimise extant correlations between means and variances. *Fidelity* is an index, being the fraction of each colony's daily incoming total trapped pollen that was cranberry. It was arcsin transformed, being a proportion. Data from four pairs of colonies were discarded owing to chalkbrood disease or foragers leaking through holes in hive equipment, both of which resulted in little or no trapped pollen.

In a second experiment involving only standard genotypes, the effect of caloric supplementation was evaluated for colony pollen influx. Cranberry flowers produce rather paltry yields of nectar (Cane & Schiffhauer, 1997). Six pairs of colonies were equalised for brood area and stores of honey and pollen. Ten days before the experiment, 500 bees per colony were given tiny marks of paint on their thoracic dorsa in the hope of censusing and comparing their foraging behaviours on the bog once they progressed to foraging tasks. Over the course of 10 days, treated colonies received 40% w/w sucrose syrup *ad libitum* from an inverted bottle with pierced lid set above the brood area; control colonies received no syrup. Syrup consumption was measured as the difference between volume fed and volume remaining. Pollen was trapped four times over the next 10 days and measured as above, and each day's difference in trapped pollen influx was compared for each matched pair and averaged over a treatment.

Results

Stigmatic pollen threshold for fruit set

The probability of cranberry fruit set increased with greater numbers of pollen tetrads on a stigma, up to eight pollen tetrads; additional pollen was superfluous for fruit set (Table 1). Only one parthenocarpic fruit formed without any pollen transfer; it was small and seedless, and therefore not recorded in Table 1. The fruit set (F) resulting from a given number of pollen tetrads being applied to a receptive stigma (T) can be described by the simple hyperbolic relationship:

$$F = 87.7\,T/(2.6 + T)$$

with a significant regression fit of $r^2 = 0.946$.

Pollination by individual honey bees

Foragers that harvested cranberry pollen actively were better pollinators than those seeking nectar alone. Honey bees that drummed flowers for pollen transferred significantly more cranberry pollen tetrads to virgin receptive stigmas than did foragers seeking nectar alone ($t = 5.00$, $P < 0.001$; Table 2). More importantly, a significantly greater proportion of flowers

Table 1. Stigmatic pollen threshold for fruit set. Percentage fruit set that resulted from pollen applied manually to cranberry stigmas.

Number of pollen tetrads per stigma	Per cent fruit set ± 95% CI†	*n*	Statistics		
			G-test comparison	*G*	*P*
0	0	43	Overall	620.74	< 0.00001
2	33 ± 13	43	8, 16 and 32 tetrads	0.43	NS
4	50 ± 15	48	4 vs. 8 tetrads	9.38	< 0.005
8	80 ± 12	45			
16	75 ± 13	44			
32	75 ± 13	44			

†Calculated 95% confidence interval (Sokal & Rohlf, 1995).

Table 2. Pollination by individual *Apis* foraging actively from cranberry flowers.

Foraging behaviour by honey bee†	Pollen on stigma after single *Apis* visit			
	⩾ 8 tetrads	Mean	SE$\bar{x}$	*n*
Pollen harvesting	86%	46.3	6.1	34
Nectar gathering	50%	13.7	2.2	58

†Pollen harvesters visibly drummed anthers for pollen; nectar gatherers also contacted the stigma but without drumming anthers.

visited by pollen-foragers would probably produce fruit ($G_{adj} = 13.84$, $P < 0.001$), as more of their visits delivered pollen in excess of the simple eight-tetrad threshold for maximal fruit set (Table 2) established by the manual pollination experiments (Table 1).

To refine the estimated contribution of the two kinds of foragers to fruit set, floral visits by honey bees were first classed into each of four of the six classes of manual stigmatic loads (i.e. < 2, 2–4, 4–8, > 8 pollen tetrads), and that fraction of the total visits was multiplied by the fruit set realised by each class of stigmatic pollen load (Table 1). By this calculation, for every 100 virgin cranberry flowers visited singly by honey bees, 77 of those worked once by pollen-foragers would yield a mature cranberry, compared with only 47 of those visited by a single nectar-forager that nonetheless made stigmatic contact. Pollen-foraging honey bees are therefore calculated to be 63% more effective in pollinating cranberries than non-thieving nectar-foragers.

Pollen foraging by honey bee colonies

Colonies headed by queens of the pollen-hoarding genotype collected significantly more pollen than like-sized colonies headed by standard queens (Fig. 1). The difference was not significant without first removing the contribution of differences in brood area as a covariate. Likewise, a colony's pollen-foraging intensity was influenced positively by its strength, as measured by area of capped brood at the end of the experiment (Table 3). The area of honeycomb with capped brood was comparable for the two genotypes; control colonies ranged from 1683 to 6174 cm^2 ($\bar{x} = 4200\,cm^2$), pollen-hoarding colonies ranged from 4037 to 5373 cm^2 ($\bar{x} = 4691\,cm^2$) of capped brood.

The daily proportion of intercepted incoming pollen that was from cranberry varied widely during the experiment, from 2 to 100% for any given colony. Some colonies consistently collected mostly cranberry pollen, both among control (e.g. 50–97%) and pollen-hoarding (e.g. 89–99%) genotypes, but fidelity of most colonies for cranberry pollen varied from day to day. In the repeated measures ANCOVA for cranberry influx, brood area and queen genotype variables were insignificant for explaining variation in daily cranberry pollen influx to individual colonies (P = NS), but the covariate of fidelity contributed significantly to daily variation of cranberry pollen influx within individual colonies ($F = 5.76$, d.f. = 3, $P < 0.01$). Overall, colonies headed by queens of the pollen-hoarding genotype collected nearly twice as much cranberry pollen as control colonies ($\bar{x} = 60.5$ vs. 35.6 g/colony). Colonies of the pollen-hoarding genotype collected significantly more cranberry pollen daily than the standard genotype, once differences in colony foraging fidelity and brood area were included in the model as covariates (Table 4).

The pollen influx of colonies fed *ad libitum* with sugar syrup remained similar to that of the paired control colonies with which they had first been matched for brood area and resource stores. On the day prior to supplemental feeding, an average of 22% more cranberry pollen was trapped from control colonies than from their paired colony destined to receive syrup (9.8 vs. 7.6 g, one colony pair excluded for a malfunctioning pollen

Table 3. Pollen foraging by *Apis* colonies. ANCOVA for the effects of queen genotype and brood area on total sampled pollen influx into honey bee colonies.

Source of variation	Sum of squares	d.f.	MS	*F*	*P*
Model	31 864	2	15 932	6.21	0.01
Error	30 783	12	2565		
Queen genotype	16 618	1	16 618	6.48	0.03
Area of capped brood	20 370	1	20 370	7.94	0.02

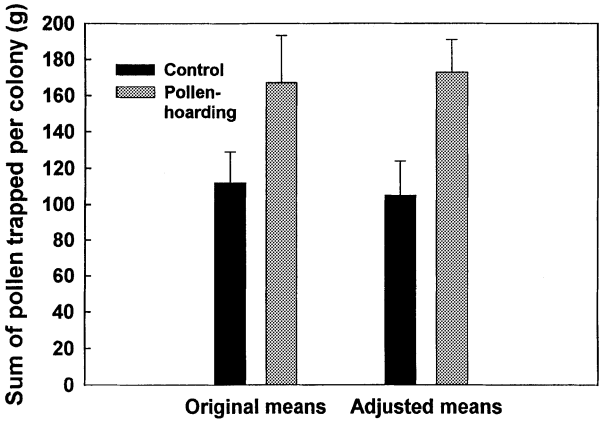

Fig. 1. Average total pollen influx (g) for five sequential samples from each honey bee colony, comparing effect of queen genotype before and after statistical adjustment for the covariate of capped brood area at the end of the experiment. Bar denotes standard error of the mean.

trap). Thereafter, control colonies continued to collect more cranberry pollen than paired colonies receiving syrup; on average, 42% more cranberry pollen was trapped from the control colonies for each pair (5.05 vs. 3.91 g). In total, 229 g of pollen were trapped, 94% from cranberry. Fed colonies consumed on average 1.2 litres of sugar syrup over the course of the experiment. None of the 6000 paint-marked hive bees was later seen foraging on the cranberry bogs, though individuals were readily found alive in their colonies on the days following marking.

Discussion

Co-evolution has been invoked as a force that moulds adaptations of plants to their pollinators and vice versa. Even if diffuse, co-evolution requires reciprocal selection on heritable characters of plants and their pollinators (Thompson, 1994). Some attributes of flowering plants showing heritable variation are known to influence pollinator host choice and preferences. Examples include both associated cues such as flower colour (Pedersen & Bohart, 1953; Goplen & Brandt, 1975; Bradshaw *et al*., 1995) and scent (Galen, 1985; Dudareva *et al*., 1996), as well as direct rewards, such as volume of nectar (Tepedino & Parker, 1982; Widrlechner & Senechal, 1992; Cane & Schiffhauer, 1997 and references therein). But do pollinators possess heritable attributes that influence that pollinator's value to plants? The salient foraging behaviours of bees are frequently overlooked, or they are assumed to be entirely plastic and without species-specific constraints or tendencies. Artificial selection reveals a genetic component to pollen-foraging by honey bee colonies that appears to have a strong influence on their contribution to cranberry pollination.

Table 4. Cranberry pollen foraging by *Apis* colonies. Repeated measures ANCOVA for effects of queen genotype, brood area, and floral fidelity on sampled influx of cranberry pollen into honey bee colonies.

Source of variation	d.f.	MS	*F*	*P*
Pollen fidelity	1	21.12	10.04	0.01
Queen genotype	1	5.48	2.70	0.06†
Area of capped brood	1	0.01	0.00	0.94
Error	11	2.04		

†One-tailed probability for colonies of the pollen-hoarding genotype collecting more pollen than control colonies.

In the work reported here, the pollination efficiencies of classes of honey bee foragers were compared by summing the probabilities of fruit set over the range of stigmatic pollen loads that they actually delivered. These probabilities were taken from the experimentally derived relationship between stigmatic pollen load and resulting fruit set. By this measure, individual pollen-foragers were 64% better cranberry pollinators than mere nectar-foragers. Some other studies have merely used the average or median count of pollen per stigma to compare pollination efficiencies of different visitors, tacitly assuming that fruit or seed production will be a 'monotonic function of pollen deposition' (reviewed by Young & Young, 1992). The regression reported here reveals that maximum fruit set is achieved with only a modest number of pollen tetrads per stigma; additional pollen is superfluous (Table 1), at least when maternal plant resources are adequate. For example, bees consistently delivering 32 pollen tetrads to a cranberry stigma were not four-fold better pollinators than those that

always delivered eight tetrads; they were equivalent. Cranberry weight was likewise maximised by a stigmatic pollen load of eight tetrads; 16 pollen tetrads maximised the set of viable seeds (D. Schiffhauer and J. H. Cane, unpublished). Only if the former bees delivered adequate numbers of pollen tetrads to stigmas more frequently might they be considered superior. The relationship advocated here is analogous to a dose–response curve in toxicology, wherein little mortality is added past the LD-90 dose of toxin; the excess is merely overkill. The relationship between pollen tetrads per stigma and fruit set for cranberry, at least, is asymptotic, not monotonic, although the location of the asymptote might shift with the question posed (e.g. competition with other maturing fruits or neighbouring flowers, timing of pollination, flower age, etc.).

Feeding honey bee colonies with sugar syrup has been explored as a means of promoting pollen-foraging. Colonies bred to hoard excess pollen or deprived of pollen stores do not field more foragers, they merely devote more of their foraging force to pollen collection at the expense of nectar foraging (Fewell & Winston, 1992; Page & Fondrk, 1995). Hence, it has been argued that feeding a colony sugar syrup should likewise free up more of the fixed foraging force to collect pollen, thus improving a colony's pollination value. Encouraging experimental results have been reported (Free & Spencer-Booth, 1961; Free, 1965; Free & Williams, 1973; Goodwin, 1986; Goodwin *et al*., 1991) but other carefully controlled experiments cast doubt on the effect (Free, 1967). A significant effect might have been expected, given the meagre production of nectar by cranberry flowers (≈ 1.4 µl of dilute nectar per virgin flower) (Cane & Schiffhauer, 1997). Colonies in this experiment on average consumed an amount of syrup equal in caloric content to the nectar production of more than a million cranberry flowers; however, despite careful pairing of colonies for previous experience, parentage, size, condition and location amid cranberry bogs, no increase in pollen foraging was observed in response to feeding syrup to colonies in this study either.

Heritable traits associated with pollen hoarding behaviours might be expected among some other bee taxa. Social species that feed or provision larvae progressively from their colony's hoarded pollen larder include all other species of true honey bee (*Apis* and *Megapis*), the nonparasitic species of tropical stingless bees (Meliponini), and many but not all species of bumble bees (*Bombus*). Taken together, these 500+ social bee taxa are influential if not dominant pollinators in most mesic continental biomes of the world, particularly the lowland tropics. Heritable traits that influence these bees' pollen-foraging behaviours are therefore likely to be significant for the fruit and seed set that they confer on their floral hosts.

Finally, this study has practical implications for pollination of cranberries and other crops using honey bees. Pollen-foraging *Apis* are markedly superior to nectar-foragers in their pollination efficiencies at apple (Free, 1966), almond (Webster *et al*., 1985), trefoil (Bader & Anderson, 1962), alfalfa (Nye & Mackensen, 1968; Mackensen & Nye, 1969), and now cranberry. As with alfalfa, some nectar-foraging honey bees will work cranberry flowers from the side, thus making no stigmatic contact. Nectar thieves were excluded from analysis in this study, as their contribution to pollination is obviously nil, owing to their failure to contact floral stigmas. Pollen-foragers are infrequent at cranberry flowers (Cane *et al*., 1993) but clearly their numbers can be increased through management (e.g. more brood, trapping pollen) or selective breeding for pollen-hoarding. Neighbouring colonies may also differ in their propensities to gather cranberry pollen (Shimanuki *et al*., 1967), possibly indicative of either differences in scouting and forager experience or underlying genetic variation, but the mechanism remains unknown. In general, selective breeding for behavioural traits of bees, such as pollen-hoarding, appears to hold more promise for pollinator improvement than some past breeding programmes that focused on morphological traits such as tongue length, the modest results of which have never been adopted by apiculturists (reviewed by Free, 1993).

A caveat regarding selection for supernormal pollen-hoarding, however, is that it has not been reported for feral or wild colonies of honey bees, even though the behaviour is manifested after just a few generations of artificial selection. The trait can impose a reproductive cost on a colony, as wax comb occupied by stored pollen is rendered unavailable to the queen for oviposition and subsequent worker production. Hence, once the volume of the nesting cavity or area of comb becomes limiting, supernormal pollen-hoarding could retard growth of a colony, delaying or diminishing its potential to reproduce by swarming.

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